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The habitat preferences of web building spiders

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Abstract

Habitat selection is an important decision to make by most species as consequences such as loss of fitness or even death can result if wrong choices are made. Web building spiders are ubiquitous species, and can be found in almost any type of environment from alpine forests to desert terrains. Factors influencing their choice of habitat is, however, still relatively unknown and has been observed to differ between populations, species and even individuals. This review will outline the main factors influencing the habitat selection of web building spiders, as well as potential constraints that may prohibit colonisation. Spiders are important components to ecosystems, providing food for a plethora of species as well as controlling levels of invertebrate prey. Understanding factors influencing the habitat selection of web building spiders is therefore important and must be studied further.

Introduction

Selecting a habitat is a decision of vital importance for animals as such decisions can have profound effects on growth, reproduction and survival (Riechert & Tracy 1975). Consequently animal distributions are often non-random, with individuals found to be more abundant in suitable habitat types where their key resources are present (Orions & Wittenberger 1991; McNett & Rypstra 2000; Voss *et al.* 2007). Site selection in most animals is often influenced through both biotic (e.g. prey availability, conspecifics) and abiotic factors (e.g. light levels, temperature, and humidity) with classical theories in behavioural ecology often suggesting that individual species respond to these factors in order to maximise their fitness (Scharf & Ovadia 2006). Web building spiders are ubiquitously found in a variety of ecosystems from tropical rainforests (Russel-Smith & Stork 1994) to desert terrains (Ward & Lubin 1993). Unlike other predators that actively hunt and pursue their prey, web building spiders have adopted a sit and wait predatory method, producing silk traps to capture their victims. Spiders are considered to be generalist feeders that primarily consume invertebrates and have a strong carnivorous tendency (Nentwig 1983; Rypstra 1986). Web building spiders can be categorised into five basic groups judging by the characteristics of their webs: the orb, tangle, sheet, tube and the funnel web (Prestwich 1977). The production of a web is a costly procedure these costs can, however, vary depending on the type of web weaving spider. Orb weaving spiders have been observed to ingest silk as they take down their webs and recycle the material to construct future webs (Opell 2002). Linyphiidae and Agelenidae, however, construct a more permanent, and costly, web (Janetos 1982).

Spiders like most animals must choose an optimal habitat that will maximise growth and reproduction as well as facilitate their survival (Scharf & Ovadia 2006). The selection of a poor quality habitat will result in reduced fitness and lower probability of survival. Spiders will want to avoid frequently relocating to find the optimal site as this process is energetically demanding (e.g. movement and web building) (Nakata & Ushimaru 2004; Miyashita 2005). Spiders are often influenced through the presence of biotic and abiotic factors providing cues to the quality of a habitat (Voss *et al.* 2006). The most influential factor in determining their distributions is, however, the source of some contention (Henschel & Lubin 1997; Chmiel *et al.* 2000; Hardwood *et al.* 2003).

This review aims to highlight the key factors influencing the habitat selection of a web building spider, with mention to the benefits gained choosing a site based on a certain factor as well as different physiological and environmental constraints that may prohibit colonisation of a preferred niche.

Web building spiders play a key role in ecosystems, providing food for a variety of other animals, as well as use of their predatory role for biological control agents reducing pest problems in agroecosystems (Oelbermann & Scheu 2009; Hardwood *et al.* 2003). Understanding their habitat preferences is thus a vital necessity which will need further exploration in future research. The concluding part of this review will, therefore, emphasise the need to carry out future projects in order to help further our understandings on the habitat preferences of the web building spiders.

Prey Availability

The factor considered to be most influential to predators when selecting a habitat is the availability of prey (Janetos 1986). Prey provides energy that can be used for

reproduction, growth and fitness. Evidently increased egg production and growth has been observed in web building spiders in association with the abundance of prey (Lubin & Henschel 1996; Hardwood *et al.* 2003; Mestre & Lubin 2011; Butcher & Entling 2011). Studies have observed spiders to strongly respond to prey abundance by choosing sites with high prey availability (Rypstra 1985; Chmiel *et al.* 2000; Hardwood *et al.* 2003; Thevenard *et al.* 2004) and have been observed to relocate their nests in response to low rates of prey arrival (Nakata *et al.* 2003; Nakata & Ushimaru 2004; Miyashita 2005).

The availability of prey is, however, stochastically variable and choosing a site based on this factor would mean having to relocate web sites frequently, which is a risky and costly process, therefore, best avoided (Nakata & Ushimaru 2004; Miyashita 2005; Ruch *et al.* 2011). Moreover a spider can only determine prey abundance at a site through experience and obtaining this experience involves producing a web (Vollrath & Houston 1986; Schuck-Paim & Alonso 2001). Johnson *et al.* (2011), however, observed the chemical cues left behind by the Desert Black Widow *Latrodectus hesperus*’s preferred prey items to provide information into the quality of the site thus influencing their choice in microhabitat selection. Spiders may therefore be able to judge a site with the use of sensory cues to determine prey quality.

Sit and wait predators, unlike most predators, have the ability to survive long periods of low prey availability by reducing their metabolic rates (Anderson 1970). Anderson (1974) observed the wolf spider Lycosid *Lycosa lenta* to survive starvation for an average of 208 days and the cribellate web-building spider *Filistata hibernalis* for an average of 276 days under laboratory conditions, with the ability to reduce their metabolic rates by around 30% to 40%. Therefore prey as the primary factor influencing the habitat selection of spiders has been heavily debated (Bradley 1993; McNett & Rypstra 2000; Scharf & Ovadia 2006).

The surrounding environment has been suggested to strongly influence a web-building spider’s ability to cope with starvation periods. Studies have observed spiders found in relatively prey rich environments to have higher metabolic rates and starvation mortalities, and are more likely to relocate in response to prey shortages in comparison to spiders found within relatively prey-poor environments (Vollrath 1985; Gillespie 1987; Ward & Lubin 1993); this has also been observed in other sit and wait predators such as the Antlion (Crowley & Linton 1999). Another possible reason for the differences in relocating in response to low levels of prey could be due to the probability of finding another site with prey available. In the prey rich site the probability is greater therefore the costs to move are far lower than spiders found within the prey poor sites (Scharf & Ovadia 2006).

Vollrath and Houston (1986), however, tested this theory with *N. clavipes* using laboratory based studies. No differences were found between the giving up times and the site tenacity of spiders reared on both prey rich and poor diets. The spiders were observed to leave sites at random, ignoring experiences gained at previous sites.

Web building spiders have been observed to differ in their prey preferences which could explain possible differences in microhabitat distributions (Nyffeller 1999). Knowing these specific prey preferences could help explain and predict their spatial

distributions. Hardwood *et al.* (2003) observed niche partitioning in two different Linyphiidae subfamily species Linyphiinae and Erigoninae. Linyphiinae locates its web just above the ground whereas Erigoninae is less web-dependent distributing its web on the ground. Results indicated that spiders place their webs in areas of high prey abundance most suited their foraging strategies. For instance there were significantly more collembola present at web-sites of the surface hunting Erigoninae and by contrast a significantly greater number of aphids and Thysanoptera were found at Linyphiinae sites. There have also been cases of extreme specialism in certain web building spiders such as the Bolas spider. This species has evolved to eat only male moths (Haynes *et al.* 2002).

Conspecifics and Competition

Spiders have been observed to use their conspecifics as a cue to the quality of a site. Hodge and Storfer-Isser (1997) investigated whether conspecific attraction to silk was a mechanism of web-site selection leading to aggregation in two species of web-building spiders *Hypocbifus thorellimmarx* and *Achaeearunea tepidarium*. They conducted three field experiments to test this theory: no spiders or webs present (cue removed), vacant webs present, and occupied webs present. In the case where no webs were present there was no tendency for the spiders to choose previously occupied sites. When vacant webs were present, spiders chose to occupy the webs. When occupied webs were present, the spiders either invaded webs and evicted the owners, or settled adjacent to and attached their webs to those of their residents.

Schuck-Paim and Alonso (2001) investigated the reasons as to why the orb weaving spider *Nephilengys cruentata* chose their habitats based on conspecifics, with the hypothesis that they do so in order to increase anchorage support for their own webs. Sites with conspecific webs as well as artificial webs were used to test this theory. *N. cruentata* was observed to settle in areas containing spider silk rather than artificial silk, thus concluding spiders to be greatly influenced by their fellow conspecifics.

Vetter and Rust (2010) tested the conspecific preference of the web building spiders *Loxosceles resula* and *Loxosceles laeta* by using own species site selection or congeneric species; neither showed a species-specific preference. However, when sites were coated with either conspecific silk or distantly related silk by the cribellate spider *Metaltella simon*, conspecific silk was favoured.

In colonial spiders conspecific webs have been thought to influence the habitat selection of juvenile spiders on dispersal. In a controlled experiment Rao and Lubin (2010) observed dispersing spiders to remain longer and build webs faster in trees that contained conspecific webs than in trees without. They proposed that spiders benefit from establishing webs in the proximity of other spiders, while dispersal to another tree may not result in arrival at an improved habitat.

Within high aggregations, spiders may be constrained from choosing their optimal sites due to competition with conspecifics. As Morse (1980) emphasised, habitat utilisation may not necessarily follow from habitat selection; if populations are large and resources are limited, intra and interspecific competition can exclude animals from preferred habitat patches. The production of larger webs may also be an indirect response to competition, depleting the prey abundance of their neighbours.

This is known as shadow competition (Linton *et al.* 1991) and has been exhibited in a variety of web building sit and wait predators (Scharf & Ovadia 2006).

However, reduced competition has been observed if sites provide enough resources. Rypstra (1986) observed reduced competition in response to greater prey resources in the Theridiidae species *Achaearanea tepidariorum*. Two groups were given differing amounts of prey. The number of spiders in enclosures dropped during the first six days in both groups. However, a higher rate of cannibalism in the low prey group caused spider numbers to drop more rapidly in comparison to the high prey group. It was therefore projected that tolerance to other neighbouring web building spiders was observed in these normally solitary spiders when large amounts of prey were present. Rypstra (1989) furthered the investigation by looking at the benefits gained from group formations of *A. tepidariorum*. Using laboratory studies, observations indicated that group colonies received greater biomass of prey and greater chance of prey capture due to ricochet effects. Therefore choosing sites based on conspecifics can benefit spiders but only if there are enough resources present.

Physical Support

The physical support of the habitat is another important factor in site selection as it provides structural support for the architecture of the web. Structural support can also be judged on arrival to a site. Certain spiders depend on specific structures for the design of their webs, for instance the bowl and doily web of *Frontinella pyramitella* requires a fork like structure in which to hang the tangled threads of the knockdown trap (Janetos 1980). Argiope orb weaving species, however, are able to construct their webs in nearly any vegetation sturdy enough to bear their weight (Sholes & Rawlins 1979; Olive 1980). Spider microhabitat distributions may therefore be predicted based on the physical supports required.

The abundance of spiders has been observed to increase in response to the number of physical supports available (Halaj *et al.* 1998; Rypstra 1998; McNett & Rypstra 2000). Robinson (1981) investigated the effects of physical complexity of a habitat on the number of spider species present. Chicken wire cages were strung with jute to provide varying degrees of spatial heterogeneity. His observations discovered that increased diversity of attachment points resulted in the presence of larger numbers of web building species.

McNett and Rypstra (2000) investigated habitat structure on spider establishment of the large orb-weaving spider *Argiope trifasciata* in old field habitats of North America over two years. Three experimental manipulations were conducted. In the first experiment natural vegetation was reduced; this resulted in a reduction in the abundance of *A. trifasciata*. The second experiment involved adding structures to a simple habitat and resulting in a greater abundance of *A. trifasciata*. The final experiment involved varying the complexity of the structures; this resulted in a greater abundance of spiders. In all manipulations, spider establishment was related to the complexity of the substrate available. Over the two year period the complexity of the site increased resulting in the greater abundance of *A. trifasciata*.

Spiders associating their habitats with vegetation can gain advantages such as thermal regulations, shelter and the reliability of prey (Uetz 1979). McCreynolds (2000) observed habitat structure to have a strong influence on the orb weaving spider *Argiope aurantia*'s prey type and abundance. His findings suggested *A.aurantia* actively choose habitats based on physical structures, as an indication of the prey quality of the site.

Balfour and Rypstra (1998) investigated the relationship between habitat structure and spider density in soybean fields, managed under conservation tillage practices using low, medium and high densities of weeds. Sheet web weavers and orb weavers were found to be the most abundant spiders in plots with the highest densities of weeds. This study, therefore, indicates these species of spiders to be associated with complex habitats.

Changes in vegetation structure have been considered to have a profound effect on spider community composition. Halaj *et al.* (1998) looked at the combination of prey abundance and habitat structure on spider abundance and diversity in Western Oregon forest canopies. Results found that spider communities could easily be predicted by the biomass of foliage as well as the availability of prey.

Pearson (2008) discovered the invasion of the spotted knapweed *Centaurea maculosa* in the North American grassland caused a significant increase in the abundance of Dictyna spiders resulting in a shift in spider community composition. Native western grasslands are currently being overrun by these Eurasian forbs, which produce flowering stems that are much larger and more structurally complex and rigid, and far more persistent than those of most native forbs. Dictyna webs were found to be 2.9 to 4.0 times larger and generated 2.0 to 2.3 times higher total prey captures on *C.maculosa* than webs on *Achillea millefolium*, their primary native substrate. This resulted in the significant increase in prey capture biomass and the increased success of reproduction.

Cobbold and Supp (2011) also looked at how changes in shrub module designs could encourage changes in the distribution of the web-building spiders Theridion and Dictyn. Both species build their webs on module edges and differ strongly in terms of concealment and substrate generalisation. Theridion was observed to be significantly more abundant on elongated modules whereas the abundance of Dictyna did not respond to changes in the shape. Spiders may therefore differ in their responses to changes in alterations in physical habitat structures resulting in changes in community compositions.

Shelter

Web damage caused by biotic or abiotic factors can cause frequent relocation in web building spiders. Shelter is therefore an important factor in the selection of a habitat. Samu *et al.* (1996) found the Linyphiidae *Lepthyphantes flavipes* to have reduced web-site tenacity in response to damage by falling leaves and heavy rainfall resulting in the selection of more sheltered habitats.

Shelter is an important factor to provide protection from predators. Blamires *et al.* (2007) observed the orb weaving spider *Argiope keyserlingi* to actively select closed habitats such as sedge and anthropogenic structures, avoiding open habitats such as trees. Prey abundance was far greater in open habitats although the risk of

predation by mantid and birds was highly probable. Spiders were therefore observed to exhibit a trade-off opting for safety at the expense of reduced foraging and growth.

Voss *et al.* (2007) studied the habitat preference of the urban wall spider *Oecobius navus* investigating different habitat variables that could influence its distributions within Perth, Western Australia. Results showed there to be a significant association of its distribution with sheltered sites.

In warmer climates such as the desert, shelter can reduce thermal stress and desiccation enabling spiders to remain cooler during the warmest parts of the day. Lubin and Henschel (1990) investigated the thermal tolerances of *Seothyra* species in the Namib Desert dunes. Spiders that were prevented from retreating into burrows were prone to stress at 49 °C whereas unrestrained spiders were able to forage at 65 °C by moving between the hot surface mat and the cooler burrows.

Temperature

Temperature is an important factor in the habitat selection of web building spiders. Being ectotherms they are considered to be constrained by their thermal environment (Cobb 1994). Observations by Goldsbrough *et al.* (2004) found temperature to have a significant effect on the growth and fitness of the flat rock spider *Hemicloea major* from eastern Australia. This spider is often associated with the warmer loose surface rocks on sandstone outcrops. During laboratory experiments *H. major* was observed to increase rate of growth and development in response to raised temperatures.

Studies have also shown temperature to be an important factor in the regulation of spider activity (Humphreys 1974; Schmalhofer & Casey 1999). Cobb (1994) found the web-building spider *Oecobius annulipes*, an inhabitant of urban walls, to have a greater flight speed from predators when substrate temperatures were raised. Voss *et al.* (2007) also studied *O. annulipes* distribution in response to differing habitat variables in Perth. This spider was found to be associated with warmer substrate temperatures which could possibly be explained by Cobb's (1994) findings. Other studies on desert spiders have also observed temperature to have a significant effect on the prey capture rates and habitat preferences (Lubin & Henschel 1990; Henschel *et al.* 1992).

Tietjen (1982), however, argued temperature to have only a slight effect on the daily activity of the communal spider *Mallos gregalis*. This spider was found to be more active during night time when temperature was cooler and less active during the day when temperatures were greater.

Riechert and Tracy (1975) studied *Agelenopsis aperta* found in desert habitats. They discovered that the heat load of some areas were less advantageous than others due to extreme thermal stress during parts of the day, preventing the spider from being active. This resulted in *A. aperta* to lose opportunities to hunt by being forced to stay in its funnel in comparison to conspecifics found in areas suitable thermal areas. Therefore temperature can act as a constraint prohibiting optimal foraging within a habitat.

Li and Jackson (1995) reviewed previously published papers on the effects of temperature on the development and reproduction in spiders. They discovered that

spiders living in warmer climates can withstand higher temperatures and develop and reproduce at a faster pace in response to warm temperatures. However, spiders adapted to cooler climates develop faster in response to cooler climates and more slowly at higher temperatures. They therefore suggested spiders to have evolved to adapt to their natural environments.

Conclusion

Animal decision making is rarely optimal owing to a wide variety of constraints such as predation and competition etc. (Scharf & Ovadia 2006). This review has highlighted the factors that may constrain and influence the site selection of web building spiders. Classical theories in behavioural ecology often suggest that foragers should choose sites based on prey abundance and site quality (Charnov 1976). This theory may not always apply to sit and wait predators that are often constrained by biotic and abiotic factors (Scharf & Ovadia 2006).

Spiders have been observed to actively weigh up the costs and benefits involved with relocating when a site no longer suits their requirements (Scharf & Ovadia 2006). These costs may, however, vary between species. For instance the cost for an orb weaving spider to relocate has been considered to be far less energetically demanding in comparison to a sheet web weaver due to their abilities to recycle their own webs (Janetos 1982; Opell 2002).

Trade-offs often occurs in the process of decision making in web-building spiders. Some spiders have been observed to risk predation by foraging in an open habitat in order to maximise their energy intake, whereas other spiders have chosen sheltered habitats trading security over the availability of food resulting in reduced fecundity and growth (Blamires *et al.* 2007).

Understanding the distributions of web building spiders is a complex procedure which involves taking into account a variety of factors. I therefore emphasise the need for future researchers to have full knowledge of web building spider's physiologies as well as the natural environment in which the spider is found. Constraints need to be taken into consideration that may limit their optimal habitat selections.

There has so far been a significant amount of literature published on web building spiders distributions over the past couple of centuries with greater understandings and patterns into their distributions beginning to emerge. Our knowledge of these successful predators is essential due to their significant roles in ecosystems as both key predators and prey for a variety of species (Blamires *et al.* 2007). Agricultural industries have begun to recognise the importance of spiders as efficient biological control agents with the ability to sufficiently reduce pest problems (Oelbermann & Scheu 2009; Hardwood *et al.* 2003). Understandings of web building spiders habitat preferences is therefore necessary and can be used to provide such practices with beneficial information.

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